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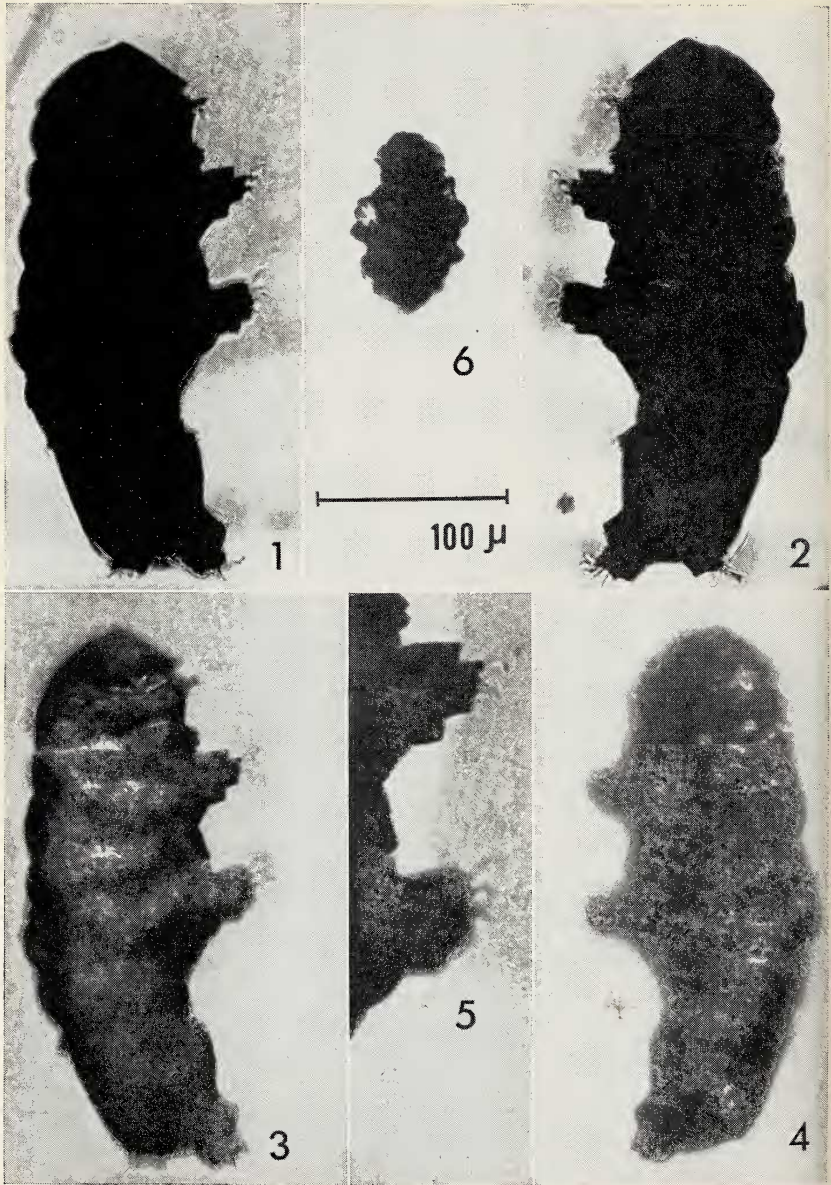
THE FIRST FOSSIL TARDIGRADE: *BEORN LEGGI* COOPER, FROM CRETACEOUS AMBER*

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In the summer of 1940, William M. Legg made a small but valuable collection of chemawinite, or Canadian amber, from sparse secondary deposits along beaches not far from the entrance of the Saskatchewan River into Cedar Lake, southeast of The Pas, Manitoba. His interest in this amber derived from the insects and other arthropods it is known to contain, for they are an extraordinary lot that very likely represent a Cretaceous fauna of some 60 to 80 million years ago (Carpenter *et al.* 1937; Holland 1951). The collection contained well over 200 zoological specimens, and its preliminary preparation and study was the subject of William Legg's unpublished undergraduate thesis in the Department of Biology at Princeton University (1942). Following his untimely death in 1953, the amber and prepared material that could be brought together was placed by his family in the collections of the Museum of Comparative Zoology at Harvard University. I had the pleasure of his friendship and of fostering his studies at Princeton; this brief study of one of the most remarkable of his specimens, and the specific name given to it, are dedicated to his memory.

Among the specimens that Legg classified in his sample are: Crustacea (copepod ?) 1, Araneida 10, Acarina 27, Thysanoptera 1, Corrodentia 3, Homoptera 43, Hemiptera 1, Trichoptera 2, Diptera Nematocera 59, Diptera Brachycera 5, Coleoptera 3, and Hymenoptera 25. Only one of these was identified by Legg with a form already described, and that is a forewing of the hymenopteron *Scerphites paradoxus* Brues (in Carpenter *et al.* 1937). This wing is a remarkable specimen because (along with a head capsule, a thorax, several legs, and a second wing—all of different insects) it had been digested free from the amber by prolonged refluxation in a Soxhlet condenser, first with absolute ethanol, then ether, and finally dioxane.

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COOPER — BEORN

Surprisingly, these specimens which had been liberated from the amber are hardly more friable or fragile than the exoskeletal remains of insects found in forest litter today.

In addition to the above, and 27 specimens of uncertain relationship, two fossils are of exceptional and general interest: a naked ciliate protozoan (Wichterman, 1953) and a tardigrade or "water-bear". The occurrence of aquatic and semiaquatic forms such as these, at first thought, may seem implausible at best. Yet Kirchner (1950) points out that large numbers of aquatic organisms have been discovered in Baltic amber in recent years, including Radiolaria, Volvocales, Cyanophyceae, corals with partially expanded polyps, and so on, and suggests that some ambers, at least, may have originated from the resin flows of swamp trees akin to cypress rather than to firs and pines. If the inclusions of chemawinite represent a swamp fauna, then the failure to find ants in the samples so far examined would have an explanation, and not require the assumption that they are of a more recent origin.

The water-bear is not to be placed in any known genus. The specimen itself lies within a small ($6 \times 7 \times 3$ mm) piece of deeply honey-colored, transparent chemawinite that is partially polished on two opposite, not parallel surfaces. Submersion in a bath of crown oil (refr. index 1.515), with illumination by reflected white light, permits its study in right dorso-lateral and left ventrolateral aspects at magnifications up to 300 diameters. A combination of transmitted and reflected light is sufficient to define the distal two-thirds of the claws of at least one of each pair of legs. The refractive index of chemawinite spans the range 1.535-1.537 (Walker 1934), and so the specimen was also studied, and all details checked, in 1, 2 dibromoethane (refr. index 1.538). Though helpful, the gain in image detail was too slight to merit prolonged use of this volatile, extremely toxic liquid. The tardigrade is placed in the genus

EXPLANATION OF PLATE 6

Beorn leggi Cooper, figs. 1-5; fig. 6 — juvenile (? hetero)tardigrade (see text).

Figs. 1, 3 — right aspect of the specimen; figs. 2, 4 — left aspect; fig. 5 — legs II and III of fig. 3, enlarged. Scale = 100 microns. Silhouettes 1 and 2 were photographed by William Legg, and are reproduced from his thesis. Figs. 3 and 4 were photographed with the specimen immersed in crown oil, illuminated with a combination of reflected and transmitted light, and in positions similar, but not identical, to those of 1, 2 and of the text figures. None of the photographs have been retouched, but the claws in fig. 5 have been given emphasis by "dodging" during enlargement.

Beorn Cooper, n. gen.

(Fig. 1; Plate 6, Figs. 1-5)

Description: Mouth without discernible palps or other appendages, dorsally and laterally enclosed by a well-defined cuticular frontal element which caps and delineates the "head"; no cephalic appendages, no lateral cirrus, no clava, and no discernible eye-spots. Body naked; cuticle evidently regionally thickened dorsally, annulated by transverse lines of flexion, but not sclerotized into distinct exoskeletal plaques either dorsally or ventrally. Legs moderately long, telescopic; each leg with four claws (or 2 two-branched claws?), and with a short, anterior, flattened, apical cuticular extension or spine, but without lateral or basal papillae.

Genotype: *Beorn leggi* Cooper, n. sp.

Origin of name: The name Beorn is that of the now storied magical bear of the Wilderland in the Third Age of Middle-earth. "Some say that he is a bear descended from the great and ancient bears of the mountains . . ." (J. R. R. Tolkien, 1937, *The Hobbit*).

Beorn leggi Cooper, n. sp.

(Fig. 1; Plate 6, Figs. 1-5)

Description: Of subaverage size: 0.3 mm long by 0.08 mm wide. Convex above, flattened ventrally. Cuticle of head without eyespots, of body smooth and without noticeable sculpture — at most very finely coriaceous; transversely crossed by four main furrows, or lines of flexion, which divide the body into five regions: P - the prostomial ("head") region, I - the first segment bearing leg pair-I ventrolaterally, II - the second segment bearing legs-II, III - the third segment bearing legs-III, and IV - the terminal segment bearing legs-IV. The relative proportions of the body regions just defined are: P (1) : II (1.3) : III (1.3) : IV (2+). Whereas each of the four major annular furrows encircles the body region, region-I has a short, transverse furrow just posterior to the middle, and regions-II and -III are each in turn divided dorsally by a secondary furrow just anterior to their midpoints; the lateral extensions of these secondary furrows fade just anterior to the base of the corresponding leg. In contrast, segment IV has a secondary furrow that extends ventrally but fades out dorso-medially.

Apically and anteriorly each leg has a short, scale-like projection of the cuticle, or perhaps flattened spine (that of leg-I being most prominent), and a cuff-like fold at midlength which strongly suggests that the leg may telescope. There are four claw-rays per leg, of which the middle two of each leg are the more dorsal. *If* the pairs of claws

are joined at their bases to form an inner (cephalad) and an outer (caudad) compound branched claw, or "diplogriffe", then the major (dorsal) branch of the inner pair is the longest of all the four elements, and the major (dorsal) branch of the outer pair is the second longest claw of each leg¹. Finally, the minor element of the inner pair of claws is larger than the minor ramus of the outer pair. Whether joined in pairs or not, the four unequal elements are obviously asymmetrically disposed with respect to the median plane of the leg.

Type: MCZ No. 5213, Museum of Comparative Zoology, Harvard University.

Type locality: One source of Legg's collection was the drift on Amber Beach, a shore that rims a small bay at the base and to the south of Oleson Point. This is in fact the site from which most of the collections of chemawinite have come. The second source, which he believed to have discovered, was the drift and debris along a beach lying due west of Oleson Point, and due south of the southern limit of the Chemawin Indian Reservation². These beaches are near to one another and to the entrance of the Saskatchewan River into Cedar Lake, and their secondary deposits are probably of a common primary origin. Regrettably no record remains from which of the two beaches the piece containing *Beorn leggi* derived.

A second tardigrade: In addition to *Beorn leggi*, the amber specimen contains a second, juvenile tardigrade (fig. 1c, d; plate 6, fig. 6). This specimen is displayed in dorsal and ventral views. Though adequate to establish its identity as a tardigrade, it is very poorly preserved, curled on itself and shriveled. There is so little detail that can be made out reliably, it does not merit description. But if there be lateral cirrus and clava as the full ventral view hints (fig. 1D), it is a heterotardigrade, perhaps an echinisoid as the *two* claws suggest which are visible from above on the left posterior leg. In any case it is evidently remote from *Beorn* in its affinities.

Relationships: Though certain morphological features of cardinal taxonomic importance cannot be made out in the specimen as it is now displayed, including stylets, buccal apparatus with its possible

¹The first three legs of the left side are displayed directly in end view in text fig. 1B, and legs 2 and 3 are similarly viewed in the photograph of fig. 4, plate 6; regrettably the optical images given by the refringent claw-rays of these legs are no more than bright beads of light at each focal level, and nothing can be made out by me of their union with the soles of the legs themselves.

²See sheet No. 63F, the The Pas Quadrangle, Department of Interior, Topographical Survey of Canada, 1927.

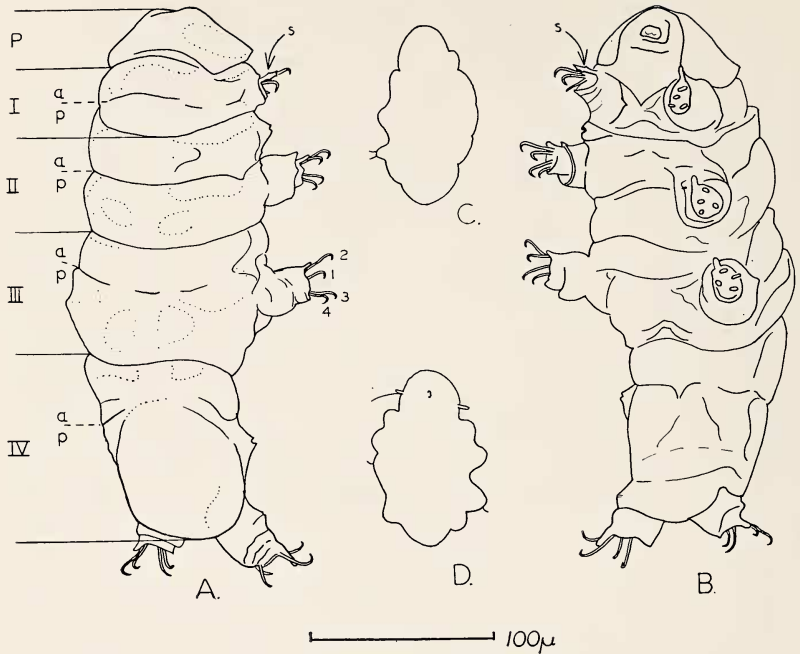


Fig. 1 A, B—*Beorn leggi* Cooper; C, D.—juvenile heterotardigrade (an echinisoid?). Compare these camera lucida sketches with the photographs of plate 6. Scale represents 100 microns.

P—"head"; I, II, III, IV—body segments bearing legs; a, p— anterior and posterior halves of segments I, II, etc., each marked off by a dorsal furrow; IVa = "pseudosegmental region" of others; s—apical cuticular projection or spine; 1 + 2—"inner" pair of claws, of which 2 is the dorsal element; 3 + 4—"outer" pair of claws, of which 3 is the dorsal element; claw $2 > 3 > 1 > 4$, see text. Dotted lines represent wrinkles and depressions.

skeletal elements, presence or absence of cloaca, or gonopore and anus, or indeed whether there are 4 claws per leg or 2 two-rayed claws, *Beorn* can nonetheless be given ordinal assignment. Though this must be done chiefly by the negative process of exclusion, the absence of cephalic appendages, of a lateral cirrus, and of a clava, are sufficient to eliminate assignment to either the Mesotardigrada (1 genus; Rahm 1937) or to the Heterotardigrada (4 families, ca. 10 genera, see Marcus 1929, 1936). The remaining order, Eutardigrada, encompasses but two recognized families: Milnesiidae (= Arctiscidae; 1 genus: *Milnesium*) and Macrobiotidae (4 genera: *Macrobiotus*, *Hypsibius*, *Itaquascon*, and *Haplomacrobiotus*). The obvious lack of rostral and lateral palps, no less the morphology of the claws

(regardless whether or not there are four, or but two, separate claw elements), eliminates the family Milnesiidae from further consideration.

If the claws of each leg of *Beorn leggi* are two in number, and if each is in turn two-rayed (that is, the individual claw is a "diplogriffe"), then it would be helpful to know whether basal lunules are present. But whether or not there are basal lunules, *Haplomacrobiotus* is eliminated as congeneric by the fact that the claws of each leg possess a total of 4 long rays in *Beorn*, and not 2 as in *Haplomacrobiotus*. Both the inequality of the rays, and the lack of rigorous symmetry of the claw rays about the median plane of the leg, and in lesser degree the sensible thickening of the dorsal cuticle in *Beorn*, set it apart from *Macrobiotus*. In these respects, and in its markedly subaverage size, *Beorn leggi* superficially calls to mind certain species of *Hypsibius*. The fossil form, however, differs sharply from the described species of both *Hypsibius* and *Itaquascon* (de Barros 1939) by the marked superiority in size of the major ramus of its inner (instead of outer) claws. Is *Beorn*, then, to be placed among the macrobiotids, more or less closely affined to *Itaquascon* and *Hypsibius*?

The family Macrobiotidae encompasses forms with strongly developed stylets and (aside from *Itaquascon*) a complicated internal buccal apparatus. Furthermore they possess gonoducts that enter the hindgut to create a "cloaca". All of these features are regrettably unascertainable in the fossil in its present state of preparation. But inasmuch as the legs of *Beorn* appear to be telescopable and provided with a distal, anterior, cuticular scale (or flattened spine), and as the pattern of the claws in any case departs from those known in the genera of living macrobiotids, it seems prudent to set the fossil form aside in a separate family, **Beornidae** (*n. fam.*), with no implication as to the possible nature of stylets, buccal apparatus, genital and anal orifices, and so on. Though telescopable legs are a feature otherwise known only in certain Heterotardigrada, it seems an insufficient character to justify creation of a new order. The Beornidae are therefore viewed tentatively as a third family of the order Eutardigrada.

At present it seems that the current major classification of the Tardigrada is not likely to be an enduring one. *Thermozodium* (Rahm 1937), for example, has a lateral cirrus but no clava, basal papillae on the legs, four peribuccal papillae, and pharyngeal skeletal elements, thus sharing cardinal features of Heterotardigrada and Eutardigrada alike. *Beorn* seems akin to eutardigrades, but possesses a telescopable leg. And within the Eutardigrada, *Itaquascon* bridges

the Milnesiidae and Macrobiotidae (de Barros 1939). In a few words, these three genera blur the distinctions that, thirty years ago, provided the Tardigrada with a clean-cut suprageneric classification.

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